Patterns in Emergence of *Acacia* and *Grevillea* Seedlings after Fire

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(Communicated by D. Keith)

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Post-fire seedling emergence was found to be pulsed in *Acacia suaveolens*, a species which is known to have its seed dormancy broken by soil heating during the passage of a fire. This post-fire establishment declines to zero some 15 months after fire. Two species of *Grevillea*, *G. buxifolia* and *G. speciosa*, showed a similar, although slightly more varied response. Hence, both *Acacia suaveolens* and *Grevillea* spp. have germination cued to the passage of a fire and are able to rapidly place seedlings into favourable sites for growth post-fire. However, seed dormancy in six *Grevillea* species was not significantly broken by heating, although temperatures of 110-120°C were lethal to seeds. In these grevilleas, the heat produced by the fire is not the cue to break seed dormancy and it is expected that some other fire-related cue (charred wood, smoke) may be responsible for breaking seed dormancy.

Introduction

Many species in fire-prone vegetation communities possess a soil seedbank. In the Sydney region of south-eastern Australia, some 89% of species in fire-prone vegetation have some form of soil seedbank. This may take the form of persistent (74%) or transient seedbanks (15%), the latter occurring where seeds have no dormancy and will germinate when sufficient moisture is available. The remaining species have either a canopy seed bank (10%) or no seedbank (1%) (Auld unpubl.). After a fire, conditions favourable for seedling growth and survival are enhanced via the release of nutrients in ash (Raison 1980), the increased availability of light and space and reduced competition levels. Consequently, the most favourable time for emergence of seedlings will be as soon as possible after a fire. This situation will favour those species that are able to respond rapidly to the passage of a fire, i.e. those species whose germination is cued to fire. There is now widespread evidence that soil heating during the passage of a fire will break seed dormancy in many plant species with a soil seedbank. This has been demonstrated in several fire-prone communities in the world in several plant families, although particularly in legumes (Cushwa *et al.* 1968; Floyd, 1966,1976; Kruger, 1983; Keeley, 1987; Jeffery *et al.* 1988; Auld and O'Connell 1991; Bell *et al.* 1993). In the Sydney region, the first seedlings to emerge after a fire are legumes such as *Acacia* spp., *Dillwynia* spp. and *Pultenaea* spp. and flushes of germination of such legumes are common after a fire (Auld, 1986). Other species which have soil seedbanks show no response to soil heating (Keeley, 1991; Auld, Keith & Bradstock unpubl.), although their seedlings may be numerous after fire. In such cases, the presence of post-fire seedlings may indicate the availability of non-dormant seed in the seedbank or the breaking of seed dormancy by other fire related cues such as charred wood (*cf.* Keeley *et al.* 1985; Keeley and Pizzorno 1986; Keeley, 1991), smoke (*cf.* de Lange and Boucher 1990; Brown, 1993), some other fire-related cue or the interaction of heat, charred wood and smoke.

For the shrub species in sandstone communities around Sydney, there is generally a

gradual decay of seeds from dormant to non dormant in the soil seedbank, independent of fire (Auld, 1986, Auld *et al.* 1993). A similar pattern exists in other coastal plants, e.g. *Acacia longifolia* (Weiss, 1984), and some semi-arid and arid plants (Grice and Westoby 1987, Auld, 1995). Consequently, two simple alternative seedbank responses after fire are possible:

1) there is a pulse of germinants after fire as a direct response to dormancy breaking cues associated with the fire. This response would be expected in many legume species where the soil heating produced during a fire breaks seed dormancy. Germination levels would be expected to decline with time since fire. Such species would exploit the favourable post-fire environment for establishment; or

2) there is no pulse of germinants after a fire as the fire has no impact on seed dormancy. The level of post-fire emergence would reflect the rate of decay of seeds in the soil from a dormant to a non dormant state. Germination levels would be expected to be fairly constant through time, although there may be pulses related to seed fall if a component of annual seed-crops are non dormant. Such species may still exploit the favourable post-fire environment for establishment if establishment is not successful at other times. This group of species would include those that show no response to soil heating or other fire cues or those species which can respond to soil heating but where soil heating during the fire has been insufficient to break seed dormancy (*cf.* Auld and O'Connell 1991).

This study aimed to examine the emergence patterns of seedlings after the passage of fire. A legume species with a known heat response, *Acacia suaveolens* (Smith) Willd. (Auld 1986) was compared to *Grevillea* species which have a contrasting seed morphology and an unknown response to heat.

METHODS

Study area

Sites were located in the Sydney Region (33°53'E, 151°13'S) of south-eastern Australia. Annual precipitation for Sydney is around 1300 mm, while the average monthly maximum/minimum temperatures are 26/18°C in summer and 16/8°C in winter.

Effect of heat on seed dormancy in Grevillea

The effect of heat on seed dormancy was examined in six *Grevillea* species. These were all shrubs comprising a component of the understorey (woodlands, forests) or dominants (heaths) of sclerophyll vegetation. Three species are common and widespread (*G. buxifolia* (Smith) R.Br., *G. linearifolia* (Cav.) Druce and *G. speciosa* (Knight) McGillivray) while the remaining three species are rare plants (*G. caleyi* R.Br. 2ECi, *G. longifolia* R.Br. 2RC- and *G. shiressii* Blakely 2VCit, codes follow Briggs and Leigh 1991, ANZECC 1993). All these *Grevillea* spp. are killed by fire and rely on germination from a soil seedbank for establishment post-fire. Two species, *G. caleyi* and *G. longifolia*, have toothbrush flowers and seeds lacking an aril (Auld *et al.* 1993), while the remainder all have 'spider-flowers' and seeds with an aril.

Field collections of seeds for each study species were made during November, December and January of 1989, 1990 and 1991. For *G. caleyi, G. longifolia* and *G. shiressii* large developing fruits were bagged and seeds were collected after the fruits had dehisced. For the other species, most fruits were collected by hand when ripe, although some bagging was done for *G. buxifolia.* In the laboratory, intact seeds were stored in envelopes at room temperature. The effect of a range of temperatures at one duration of heating on seed germination were examined in the laboratory. Ten temperature levels were examined; ambient (control), 40, 50, 60, 70, 80, 90, 100, 110 and 120°C, for a single duration of exposure (10 mins). Thirty seeds were tested for each temperature treatment,

although occasionally sufficient seeds were available to use additional seeds as replicates in the control. A small volume of air-dried soil from the field was enclosed in aluminium foil and preheated in an oven to the desired temperature. Once preheated, the soil was removed from the oven and seeds added. A thermometer placed in the soil was used to monitor the soil temperature. After exposure in the oven for the required time, seeds were extracted from the soil using a sieve (mesh 2 x 2 mm) and allowed to cool. Individual seeds were then placed on Whatman grade 2 filter paper moistened with distilled water in 9 cm diameter petri dishes. Germination was followed for eight weeks, after which all seeds which had not germinated were scarified and allowed to germinate in order to estimate the viability of the seed lot used. Any seeds which still did not germinate were tested for viability using the tetrazolium test (Lakon, 1949). Comparisons between temperature treatments were made via a two factorial model in GLIM (Aitkin *et al*. 1989) with a binomial error structure.

Seedling emergence in the field

Post-fire emergence of seedlings was recorded at four study sites in Garigal National Park in the northern suburbs of Sydney. Three of the sites were burnt in November 1992, while the fourth was burnt 2 months earlier. Vegetation at the sites was a mixture of heath and open woodland with a shrub understorey on Hawkesbury sandstone. At each site a quadrat was marked out and all emerging *Acacia* and *Grevillea* seedlings were tagged at 2-3 monthly intervals for up to 15 months post-fire. Quadrat size varied between sites and was governed by the abundance of emergents. Sampling involved repeated counts at the same quadrats over time so that each emergent seedling could be assigned to a particular time interval post-fire. It was assumed that correlations between counts from the same quadrats across time intervals were minimal. Emergent seedlings were *Acacia suaveolens* at all sites, *Grevillea speciosa* (3 sites) and *G. buxifolia* (2 sites). Patterns of emergence were examined for *Acacia* and pooled *Grevillea* spp. across time intervals using the number of seedlings emerged in a particular time interval as a fraction of the total number of seedlings emerged over all time periods. Data were analysed by a three factorial model GLIM using a binomial error structure. Appropriate post-hoc tests were made using a Z statistic (Zar, 1974). A range of curves were fitted to proportional emergence across time to estimate the best fit to the data.

RESULTS

There was no clear evidence that heating broke seed dormancy in any of the six *Grevillea* species examined (Table 1, Fig. 1). There was considerable variation in the level of non-dormant seeds between species. In all species, temperatures of 120° C were lethal to seeds, while some seed death also occurred at 110° C. Significant temperature effects in species were related to this seed death at high temperatures. The one significant Site times Temperature interaction (*G. linearifolia*, Table 1) mainly reflected different seed mortality levels at 100 and 110° C (Fig. 1c). For some species, there was a high level of seed dormancy at all treatments (*G. caleyi*, Fig. 1b), while for others, high levels of non dormancy were apparent in all treatments below the lethal temperatures (*G. linearifolia*, Fig. 1c, *G. speciosa*, Fig. 1f).

Seedling emergence patterns in *Acacia suaveolens* and pooled *Grevillea buxifolia* and *G. speciosa* were similar, with an initial post-fire pulse declining to very small to no emergence some 15 months after the fire (Fig. 2). While one site had a significant increase in seedling emergence in *Grevillea* at the second time interval compared to the first (Fig. 2b), the same overall pattern of a decline through time was apparent at all sites. This is reflected in a significant three-way interaction in the GLIM analysis (Table 2). An exponential model was the best fit to the data in terms of decline in emergence through time (Fig. 2).

These regressions accounted for 96% and 71% of the variation in emergence through time for *Acacia suaveolens* and pooled *Grevillea* species, respectively.
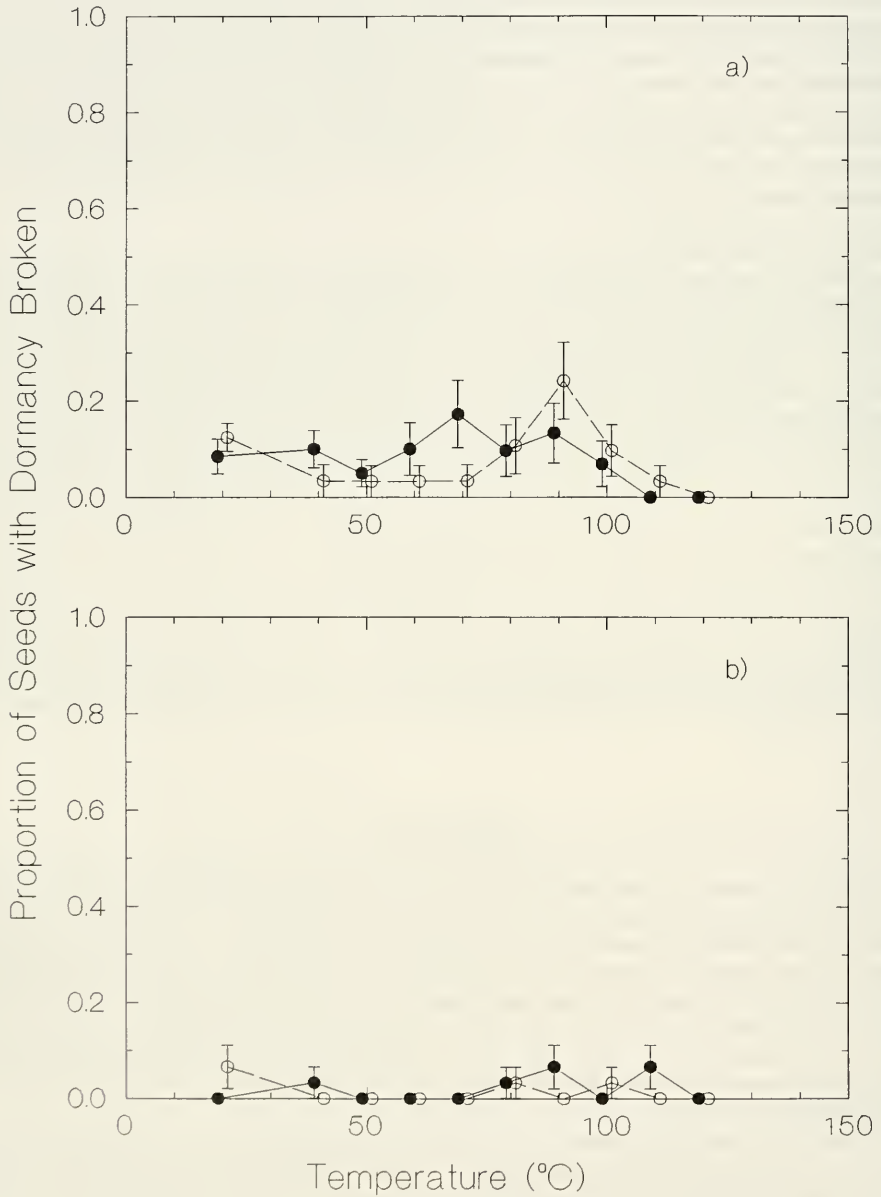

Fig. 1. Effect of heat on seed dormancy in *Grevillea* spp. Different lines represent different yearly samples and/or sites. Bars represent standard errors. The position of points on the x-axis have been adjusted slightly for clarity.
a) *G. buxifolia;* b) *G. caleyi;* c) *G. linearifolia;* d) *G. longifolia;* e) *G. shiressii;* f) *G. speciosa*
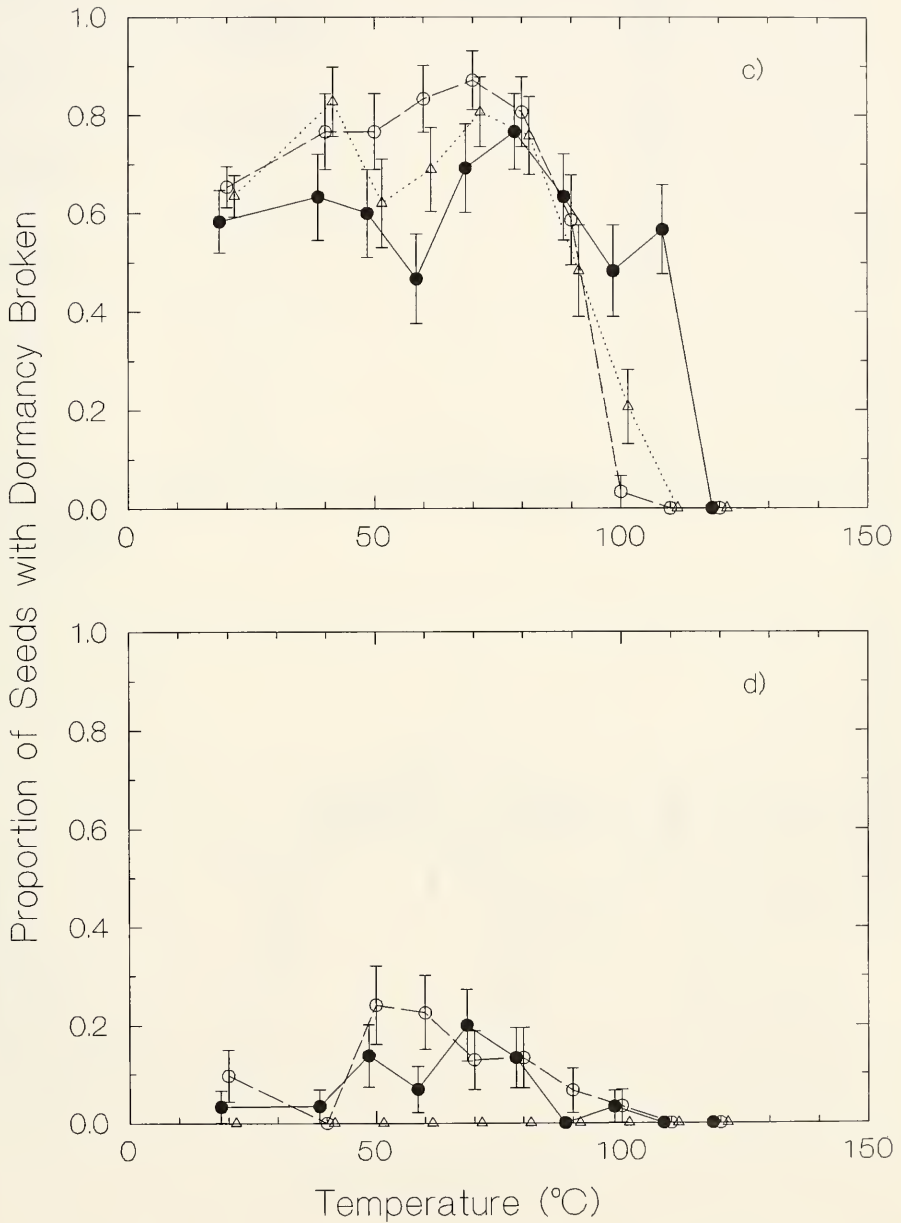
Fig. 1, cont'd. Effect of heat on seed dormancy in *Grevillea* spp. Different lines represent different yearly samples and/or sites. Bars represent standard errors. The position of points on the x-axis have been adjusted slightly for clarity. a) *G. buxifolia*; b) *G. caleyi*; c) *G. linearifolia*; d) *G. longifolia*; e) *G. shiressii*; f) *G. speciosa*
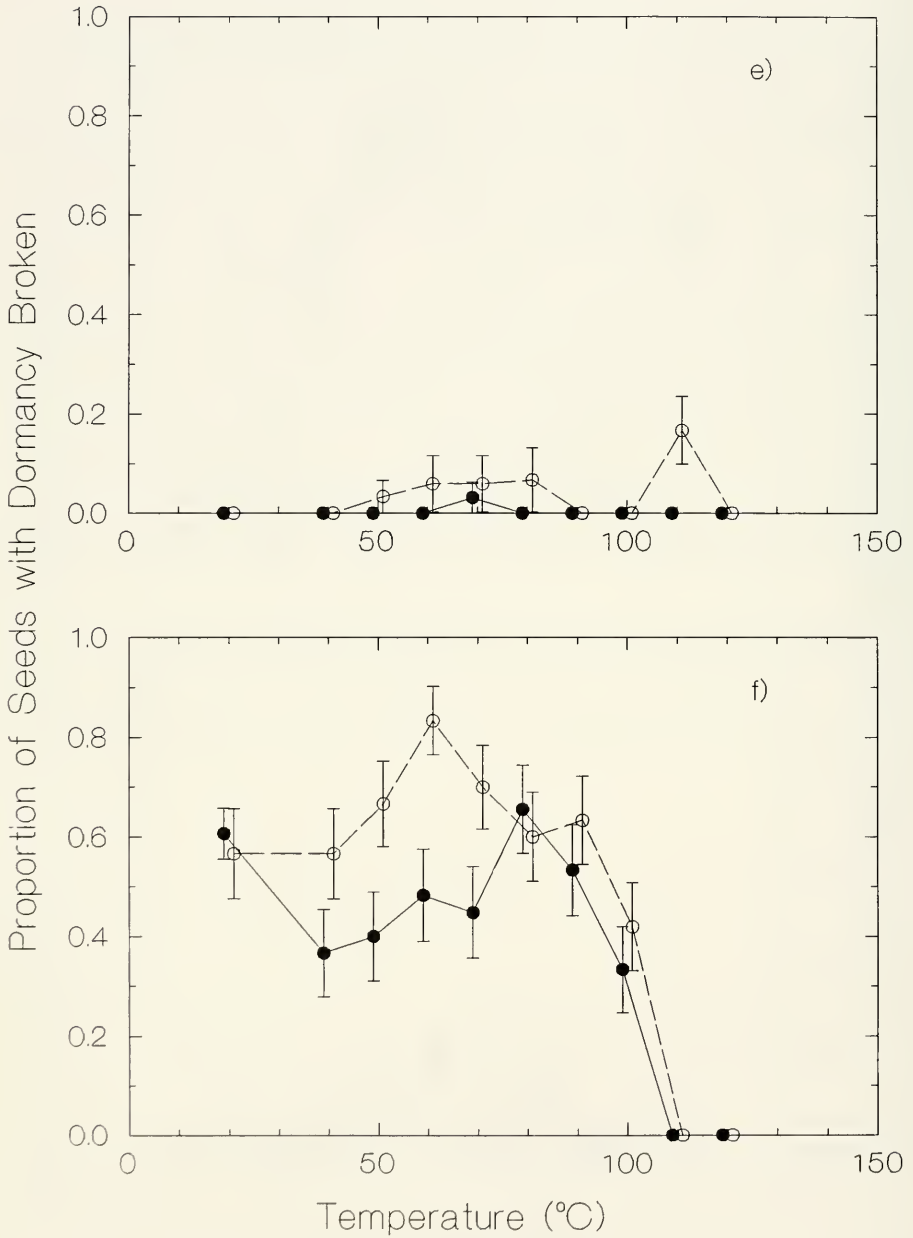
Fig. 1, cont'd. Effect of heat on seed dormancy in *Grevillea* spp. Different lines represent different yearly samples and/or sites. Bars represent standard errors. The position of points on the x-axis have been adjusted slightly for clarity. a) *G. buxifolia;* b) *G. caleyi;* c) *G. linearifolia;* d) *G. longifolia;* e) *G. shiressii;* f) *G. speciosa*

TABLE 1

Comparison of the effect of heat on seed dormancy in six <u>Grevillea</u> species using GLIM.

Species	Factor	Change df	Change dev	P[1]
G. buxifolia	Site	1	0.01	ns
	Temperature	9	26.48	**
	Site x Temperature	9	9.16	ns
G. caleyi	Site	1	0.42	ns
	Temperature	9	11.26	ns
	Site x Temperature	9	10.92	ns
G. linearifolia	Site	2	0.99	ns
	Temperature	9	304.9	***
	Site x Temperature	18	83.3	***
G. longifolia	Site	2	42.66	***
	Temperature	9	44.64	***
	Site x Temperature	18	8.17	ns
G. shiressii	Site	1	10.13	**
	Temperature	9	19.47	*
	Site x Temperature	9	3.13	ns
G. speciosa	Site	1	9.54	**
	Temperature	9	182.9	***
	Site x Temperature	9	10.9	ns

1, ns, non significant
* $0.05 > P > 0.01$
** $0.01 > P > 0.001$
*** $P < 0.001$

TABLE 2

GLIM comparisons of the proportion of seedlings emerging at various time intervals post-fire for <u>Acacia suaveolens</u> and <u>Grevillea</u> spp.

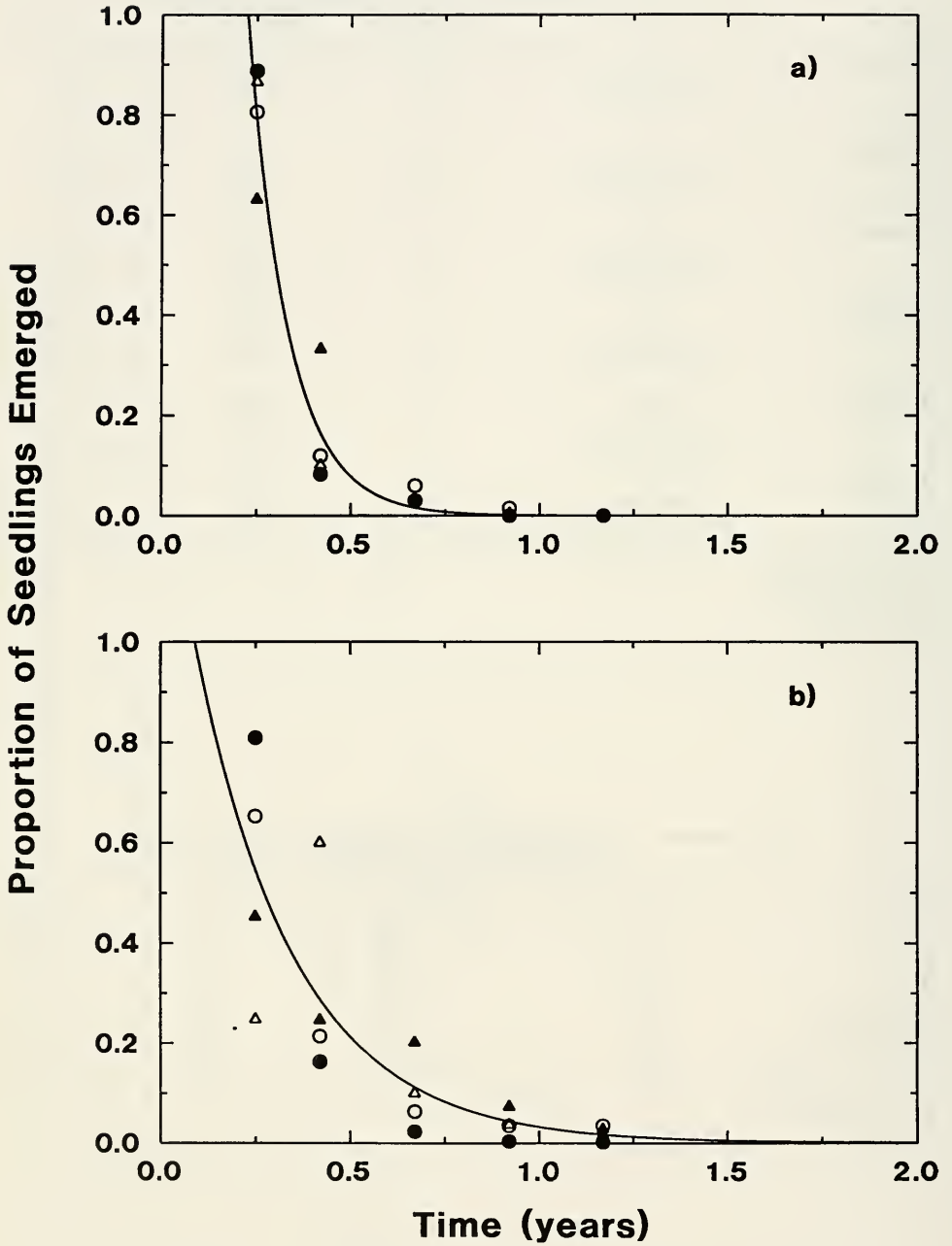| Factor	Change df	Change dev	P[1]
Species	1	0.04	ns
Site	3	0.05	ns
Time	4	3137	***
Species x Site	3	0.46	ns
Species x Time	4	76.5	***
Site x Time	12	430.8	***
Species x Site x Time	12	125.8	***

1, ns, non significant
*** *P<0.001.*

Fig. 2. Post-fire emergence of seedlings. Lines represent line of best fit (see text).
Different symbols represent different sites. a) *Acacia suaveolens*; $y = 8.117.e^{-9.285x}$
b) *Grevillea buxifolia* and *G. speciosa* combined. $y = 1.402.e^{-3.77x}$

Discussion

The *Grevillea* species examined contrast with *Acacia* spp. (see Auld and O'Connell 1991) in that they show no breaking of seed dormancy by heating. It is unlikely that longer durations of heating may have affected seed dormancy (Auld & O'Connell 1991) and such durations are not typical of soil heating in the field during the passage of a fire (Bradstock and Auld 1995). Consequently, while it would be expected that *Acacia* spp. would show a pulse of germinants post-fire, the expected response from *Grevillea* spp. is unclear. No pulse would be expected where there is no seed response to the passage of a fire. In such a situation seedling emergence is dependent upon the rate of decay of seeds from a dormant to a non dormant state in the soil seedbank. Alternatively, some cue associated with the passage of a fire apart from heat may be responsible for breaking seed dormancy. Such a cue could be leachates from charred wood (*cf.* Keeley *et al.* 1985) or chemicals derived from smoke (*cf.* Brown, 1993). Should such a fire-related cue exist in *Grevillea*, then a pulsed response would be expected.

The examination of post-fire emergence in the field confirmed the predicted pulse for *Acacia suaveolens* (Fig. 2a). The exponential regression (Fig. 2a) was able to explain some 95.6% of the variation in seedling emergence over time and is a good predictor of the likely emergence pattern in this species. Depending on the timing and magnitude of post-fire rainfall, the positioning of this curve may vary, however its shape should remain roughly the same.

For *Grevillea buxifolia* and *G. speciosa* there was also a strongly pulsed pattern of post-fire emergence (Fig. 2b). In this case, the exponential regression accounted for some 71% of the variation in emergence over time. For *Grevillea* species there was more variation between sites in the initial magnitude and timing of the pulse, however, the overall pattern was strikingly similar to *A. suaveolens*. In the case of *Grevillea* spp., the breaking of seed dormancy by heating of the soil during the passage of the fire cannot be invoked to explain the observed response. Clearly, there is a distinct post-fire pulse of germinants but the fire-related factor responsible for breaking seed dormancy remains unknown. It is possible that *Grevillea* spp. respond to fire cues such as smoke or leachates from charred wood and this remains an interesting area for future research.

Auld and O'Connell (1991) predicted that the amount of the soil seedbank that is stimulated to germinate by the passage of a fire in species with dormancy broken by heat will vary depending on the amount of soil heating that occurs during a fire. This in turn is controlled by the amount of fine ground fuels that are burnt during a fire, a component of fire intensity (Bradstock and Auld 1995). In general, fires with high levels of fine fuel combustion will cause the greatest depletion of the soil seedbank through high post-fire germination levels. Following from this, patterns of the depth of emergence of seedlings should be closely tuned to small-scale litter and fine fuel patterns. Predicted levels of seeds emerging from the soil seedbank in *A. suaveolens* range from 1.1 to 32.9%, depending on the amount of soil heating that occurs (Auld and O'Connell 1991). Additional seeds near the soil surface will be killed by lethal temperatures. Clearly under this scenario, seeds will be depleted from certain depths and remain available at greater depths, depending on the level of soil heating, i.e. there is a soil depth-related impact for species whose seed dormancy is broken by heat. It remains to be seen whether an equivalent soil depth-related response occurs in species whose dormancy is broken by a fire-related cue other than heat, although the seedbank will be depleted at the soil surface as seeds are killed by soil heating.

The relative speed with which seedlings of particular species emerge in the post-fire environment will reflect their strategy of seed storage between fires and whether a persistent seedbank is maintained or not. Species that store seeds in the soil and have persistent seedbanks are likely to be the quickest to place seedlings in the favourable post-fire environment if they have their dormancy broken by the passage of a fire. Species with a canopy seedbank must wait for seeds to be released from the woody cones, and this may take many

weeks after the fire has passed. Species that rely on dispersal from outside the burnt area must wait for the season of fruit maturation in unburnt communities and this will not necessarily coincide with the favourable immediate post-fire period. Finally, there are those species that have transient soil seedbanks and that rely on a post-fire pulse of flowering to place seedlings in the post-fire environment. These species may take from a few weeks up to 2 years to flower after fire and therefore are the slowest to place seeds in the post-fire environment.

For species with a soil seedbank, the pattern of post-fire emergence of seedlings should reflect moisture conditions, the influence of fire (heat, charred wood, smoke etc.) on breaking seed dormancy, and the breaking of seed dormancy by means other than the passage of the fire. While *A. suaveolens* and *Grevillea* spp. have different mechanisms for having seed dormancy broken in relation to a fire, this makes no difference to the timing of the post-fire pulse of emergent seedlings. This may be because both dormancy breaking mechanisms operate at the time the fire passes. Alternatively, as seeds must wait until there is sufficient moisture in order to germinate, any differences between the timing of dormancy breaking by different fire-cues may be eliminated.

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